A New Subspecies of the Schoolmaster Gonate Squid, *Berryteuthis magister* (Cephalopoda: Gonatidae), from the Japan Sea

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Abstract. Morphological and genetic variation of the gonatid squid *Berryteuthis magister* from the North Pacific Ocean is analyzed. Geographical differences were observed between sexually mature squid from different parts of the species range. *B. magister* from the Japan Sea was clearly distinguished from other conspecific populations by distribution of several morphologic features: dorsal mantle length, nidamental gland length, fin length, and fin width. Genetic divergence D_N between squid from the Japan Sea and from waters off the Kurile Islands was 0.044, as revealed from 26 protein-coding genetic loci. Significant allele frequency differences were observed at seven of 12 polymorphic loci, and gene differentiation F(ST) equalled 0.12. Data from morphology, genetics, geographical distribution, reproduction, and ecology suggest that *B. magister* from the Japan Sea constitute a separate taxon of subspecific rank. *Berryteuthis magister shevtsovi* subsp. nov. from the Japan Sea is described. The subspecies is small, with a large fin, a bicuspid lateral tooth on radula, and weak differentiation between the central and marginal suckers on the tentacular club. It breeds in spring, and produces a small number of large eggs. It leads a bathypelagic life in the Japan Sea at very low temperatures.

INTRODUCTION

The schoolmaster gonate squid *Berryteuthis magister* (Berry, 1913) is the type species of the genus *Berryteuthis* Naef, 1921. Specimens of this squid were first described by Berry (1912) from Puget Sound, and were identified at that time as *Gonatus fabricii* (Lichtenstein, 1818). Berry noted that they differed from true *G. fabricii* in several features, the hookless tentacular club being the most notable. A year later (Berry, 1913), the specimens received specific taxonomic status as *Gonatus magister* Berry, 1913. Based primarily on tentacular club armature and radula morphology, Naef (1921) placed this gonatid species in a new genus *Berryteuthis*. It was not until the discovery and description of several other gonatid species that taxonomic validity of the genus became obvious, and was accepted by malacologists (Okutani, 1968; Roper et al., 1969). Pearcy & Voss (1963) described the species *Gonatus anonychus,* which shared with *B. magister* such generic characters as a hookless club and a radula with seven teeth in a transverse row (septemdentate). Okutani (1968) later placed *G. anonychus* into the genus *Berryteuthis.*

Berryteuthis magister is presently considered a polytypic species with two subspecies: *B. (m.) magister* (Berry, 1913), and the recently described *B. (m.) nipponensis* Okutani & Kubodera, 1987 (Okutani et al., 1987). The Japanese subspecies is extremely rare, with only three specimens known so far, which were caught in Japanese waters in the Sanriku region (holotype specimen), Toyama Bay (Okutani et al., 1987), and off Cape Erimo (Kubodera, 1993). All specimens of *B. (m.) nipponensis* are immature, and can be distinguished from the typical *B. magister* by the presence of a muscular mantle with small mantle opening (pallial aperture), small fins, and less pronounced size differences between central and marginal suckers on the club (Okutani et al., 1987). The nominotypical subspecies is very abundant in the North Pacific, and has a wide geographical distribution, including marginal basins, such as Japan, Okhotsk, and Bering seas, and the Gulf of Alaska (Nesis, 1987). *B. (m.) magister* from the Japan Sea is apparently a geographical isolate, which lives under rather specific hydrological conditions (Okiyama, 1993), and exhibits peculiarities both in reproductive cycle (Nazumi et al., 1979; Yuuki & Kitazawa, 1986; Natsukari et al., 1993), and morphology.

The analysis of certain morphologic characters, together with the analysis of inherited molecular variation as revealed by protein electrophoresis, provided reliable evidence in favor of taxonomic separation of *B. (m.) magister* from the Japan Sea on a subspecific level when compared with *B. (m.) magister* from other parts of its distribution range. A new subspecies of *B. magister* is described.

MATERIALS AND METHODS

A total of 3501 specimens of squid were used for the analysis of intraspecific differences. All were morphologically identified as *B. (m.) magister,* hereafter referred to as *B. magister* (Figure 1, Table 1). Three thousand one hundred and seventeen specimens in 14 sample lots were taken for the size composition comparison of *B. magister* from different regions of the North Pacific Ocean: Japan
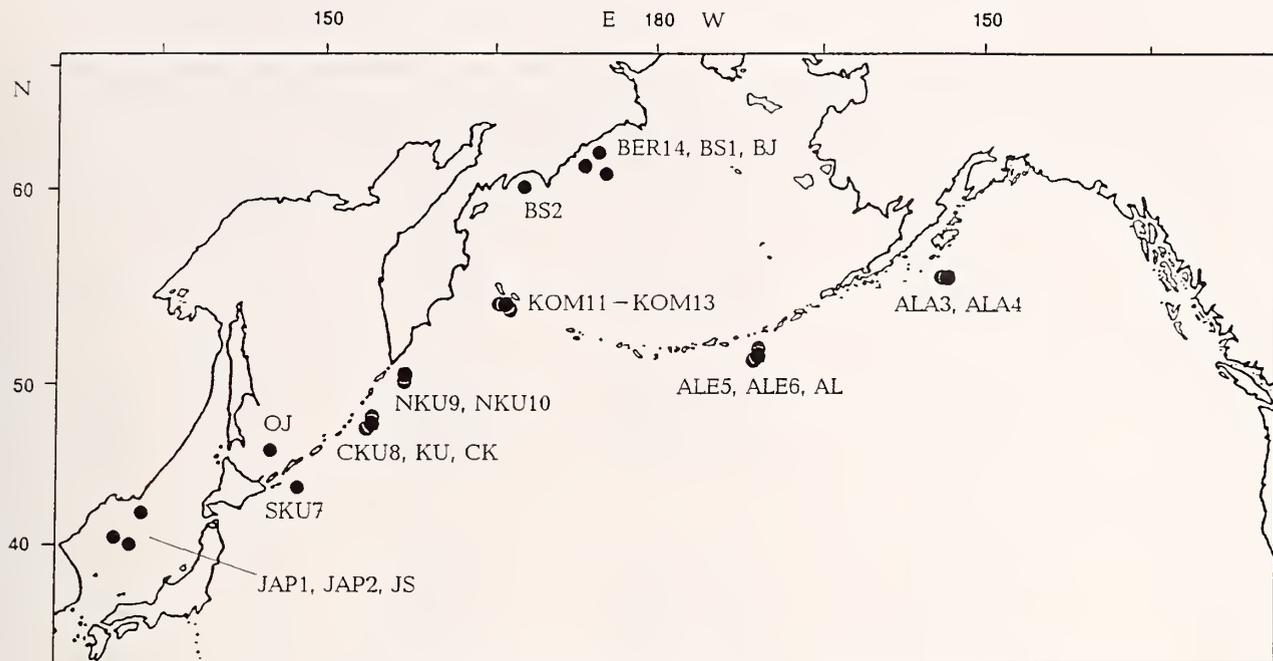
Figure 1

Berryteuthis magister. Location of samples in the North Pacific Ocean.

Sea (Kitayamato Bank); Pacific waters off the Kurile Islands; the Kommander Islands (central bank); the northwestern Bering Sea (Olutorsko-Navarinskyi Region); and the northeastern Pacific (central part of the Aleutians and Gulf of Alaska). All specimens were sexually mature, which suggests that squid were taken from breeding stocks. Squid from the Japan Sea and the northwestern Pacific which were subjected to size composition analysis were caught during 1988, whereas those from the northeastern Pacific Ocean were caught in 1985 and 1987. One hundred and sixty specimens in seven sample lots were taken for the analysis of fin proportions of immature and mature *B. magister* from the North Pacific Ocean.

Morphology of the radula was studied in mature specimens from the Japan Sea (25 specimens), and in mature and immature specimens from the northwestern Bering Sea (25 specimens) under light microscope and under scanning electron microscope (SEM) JEOL JSM-25SII. Soft tissues of the buccal mass were macerated in 10% NaOH for 24 hr. The radular ribbon was then removed, washed in tap water, and placed in 70% ethanol. Radular structures were resolved under SEM with accelerating voltage of 25 kV, and with a magnification of 70×.

A total of 234 *B. magister* specimens in two sample lots, representing two geographical regions, the Japan Sea, and the northwestern Pacific, were taken for electrophoretic comparison of enzyme-coding genetic loci. Details of multilocus electrophoretic analysis for the squid are described elsewhere (Katugin, 1991, 1992, 1993, 1995, in press; Katugin et al., 1992). Abbreviations of genetic loci, revealed by protein electrophoresis, were for the most part conventional, and were used following general recommendations suggested by Allendorf & Utter (1979). Basic calculations were made using a BIOSYS-1 computer program (Swofford & Selander, 1981, 1989). The following standard variability measures were used: mean sample size per locus, mean number of alleles per locus, two criteria of polymorphism (0.95 and 0.99), and mean heterozygosity per locus (biased, unbiased, and direct-count estimates). Contingency comparison was conducted by chi-square test (Workman & Niswander, 1970), and genetic differentiation was assessed using F(ST) (Wright, 1978). Standard genetic distance D_N (Nei, 1972) was used to measure proportion of codon differences between geographical populations. Estimation of presumptive intersubspecific divergence time (t) was made using Nei's formula: $t = 5 * 10^9 D_N$ (Nei, 1987).

Specimens used in the description of the new subspecies were fixed in a 5% formaldehyde solution for 7 days followed by transfer to 45% isopropanol solution for long-term preservation.

RESULTS

Size Composition

Mature specimens of *B. magister* exhibited a geographical pattern with regard to size: dorsal mantle length (DML) range and mean for males and females were the

Table 1

Berryteuthis magister: Locations, dates, and number of sampled specimens. Abbreviations: AM—mature adults; AI— immature adults; JU—juveniles; *—samples for size composition analysis; **—samples for fin dimensions analysis; ***—samples for multilocus electrophoretic analysis.

Sample	Region	Coordinates	Date	Number	Maturity
Japan Sea					
JAP1*	Kitayamato Bank	39°56′N 133°53′E	8.02.1988	434	AM
JAP2*	Kitayamato Bank	39°59′N 133°49′E	12.04.1988	137	AM
JS**, ***	Russian Primorie	42°30′N 133°42′E	23.05.1996	104	AM, AI
North-eastern Pacific Ocean					
ALA3*	Gulf of Alaska	55°27′N 155°46′W	27.06.1985	24	AM
ALA4*	Gulf of Alaska	55°37′N 155°25′W	26.06.1986	15	AM
ALE5*	Aleutian Islands	53°15′N 165°20′W	13.06.1985	89	AM
ALE6*	Aleutian Islands	53°43′N 165°10′W	15.06.1987	11	AM
AL**	Aleutian Islands	53°05′N 171°36′W	24.03.1989	20	AM, AI
North-western Pacific Ocean					
	Kurile Islands				
SKU7*	Southern Kuriles	44°48′N 148°53′E	15.05.1988	168	AM
CKU8*	Central Kuriles	46°51′N 152°06′E	11.05.1988	29	AM
KU**	Central Kuriles	46°50′N 152°06′E	14.09.1996	43	AI
CK***	Central Kuriles	47°12′N 152°29′E	8.11.1991	133	AI
NKU9*	Northern Kuriles	49°46′N 154°57′E	19.06.1998	95	AM
NKU10*	Northern Kuriles	49°40′N 156°62′E	7.07.1988	223	AM
OJ**	Okhotsk Sea	45°23′N 145°35′E	2.06.1988	17	JU
	Kommander Islands				
KOM11*	Central Bank	54°30′N 167°05′E	28.01.1988	202	AM
KOM12*	Central Bank	54°24′N 167°06′E	22.05.1988	407	AM
KOM13*	Central Bank	54°29′N 167°02′E	1.12.1988	1154	AM
	Bering Sea				
BER14*	Navarin Region	61°40′N 176°30′E	17.09.1988	129	AM
BS1**	Navarin Region	61°23′N 175°23′E	4.09.1996	20	AM
BJ**	Navarin Region	61°43′N 176°36′E	9.09.1996	23	JU
BS2**	Olutorsky Bay	60°02′N 168°38′E	8.09.1996	20	AM

lowest in samples from the Japan Sea (Figure 2). Mean size for males was 150.2 ± 0.7 mm in February, and almost the same, 151.5 ± 3.8 mm, in April. Females in February were smaller than in April, having a mean DML of 180 ± 0.7 and 192.2 ± 1.7 mm, respectively. Size differences were significant ($P < 0.001$), which could be explained by a higher proportion of mated females in April (84%) than in February (11%). Mated females with traces of copulation (ropes of spermatangia implanted in the inner wall of the mantle) had a mean size of 189.7 ± 1.8 mm in February and 193.8 ± 2.0 mm in April, showing no significant differences. In the western and southwestern Japan Sea, DML values for copulated females were almost as low as in the central part, with a mean value of 195.6 ± 2.5 mm for specimens from the Oki Bank (based on data from Nazumi et al., 1979). In the northeastern and northern Japan Sea off the Russian Primorie coast, mature squid were somewhat larger, with DML values of 177.1 ± 4.0 mm for males and 207.6 ± 3.8 mm for females (P. P. Railko, personal communica-

tion). Among 440 prespawning females sampled by Dr. G. A. Shevtsov in February through May 1988 from the Kitayamato Bank, seven (1.6%) specimens had DML larger than 220 mm, one of them with a maximum value of 315 mm. Mean DML for copulated females was 194 mm, with a mode of 202 mm. Among 320 ripe males, eight (2.5%) had DML larger than 170, and the maximum value for one of them was 202 mm.

Geographical trends in size distribution were also observed for *B. magister* from the northwestern Pacific Ocean: the largest specimens were present in the southern part of the region, and mean size generally decreased northward (Figure 2). Both males and females caught off the southern Kuriles were very large with mean DML values of 245.9 ± 1.8 and 313.7 ± 6.3 mm, respectively. The smallest males with mean DML of 205.1 ± 1.5 mm were from the northern Kuriles, and the smallest females with mean DML of 253.3 ± 1.3 mm were from the Bering Sea. Squid from the northeastern Pacific region were characterized by their very large size when compared
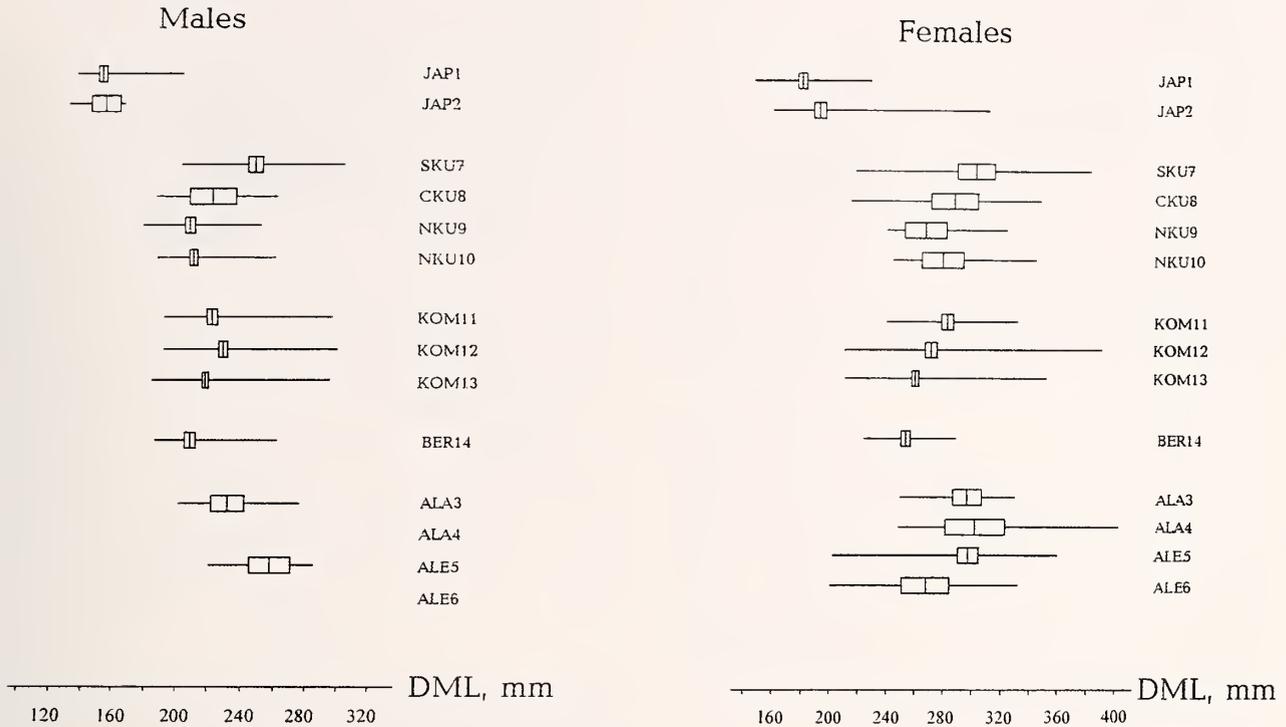
Males

Females

Figure 2

Berryteuthis magister. Size distributions of mature males and females from the North Pacific Ocean. DML, dorsal mantle length; vertical line, mean; rectangle, 95% confidence limits; horizontal line, range.

with conspecific populations from the other regions. In the northeastern Pacific Ocean, the largest males were collected off the Aleutian Islands with mean DML of 257.5 ± 6.1 mm, and the largest females were found in the Gulf of Alaska with mean DML of 301.1 ± 11.2 mm. In a sequence of regions—the Japan Sea, the northwestern, and northeastern Pacific–respective mean values of DML were 150.3 ± 0.7, 224.9 ± 0.6, and 242.9 ± 4.5 mm for males, and 184.2 ± 0.8, 273.5 ± 0.9, and 294.0 ± 3.0 mm for females.

Size distribution graphs for mature *B. magister* revealed some regional-specific features (Figure 3). One of the most striking features is a gap between size distribution curves for specimens from the Japan Sea and from other regions of the North Pacific Ocean. DML distributions for males and females from the Japan Sea are almost unimodal with modal classes 150–160 and 180–190 mm, respectively. Males larger than 190 mm, and females larger than 220 mm were extremely rare. In the northwestern Pacific there are main modal classes of 220 mm for males, and 270 mm for females with a pronounced proportion of large animals. Total share of females with DML larger than 300 mm constituted up to 20% of all ripened females in the spawning stock off the Kommander Islands. In the northeastern Pacific unimodality of size distribution is even less evident. Two size groups of *B.*

magister were present in different ratios in the Aleutians and in the Gulf of Alaska: small squid with equal modal classes for males and females of 210 mm, and large squid with modal classes of 270 mm for males and 300 mm for females.

On the scatterplot of DML against nidamental gland length (NGL), a geographical pattern is also seen. Measurements of both characters separated sexually mature squid from the three regions of the North Pacific Ocean (Figure 4). Squid from the Japan Sea occupy a distinct separate zone on the graph, while distribution patterns for specimens from the northwestern and northeastern Pacific overlap considerably. Mean DML values for *B. magister* from the Japan Sea, northwestern, and northeastern Pacific were, respectively, as follows (values for males are given in parentheses): 184.2 ± 0.8 (150.3 ± 0.7), 273.5 ± 0.9 (224.9 ± 0.6), and 294.0 ± 3.0 (242.9 ± 4.5) mm. Mean NGL values for females were 78.2 ± 0.5, 107.1 ± 0.4, and 126.2 ± 1.7 mm, respectively.

Line, or simple regressions, of NGL by DML, for squid from all the three North Pacific regions are as follows: 5.91 + 0.39 * DML (Japan Sea), 45.0 + 0.23 * DML (northwestern Pacific), and 61.7 + 0.22 * DML (northeastern Pacific). First coefficients do not vary significantly between the last two regions, and were significantly different ($P < 0.0001$) from that of the Japan Sea.
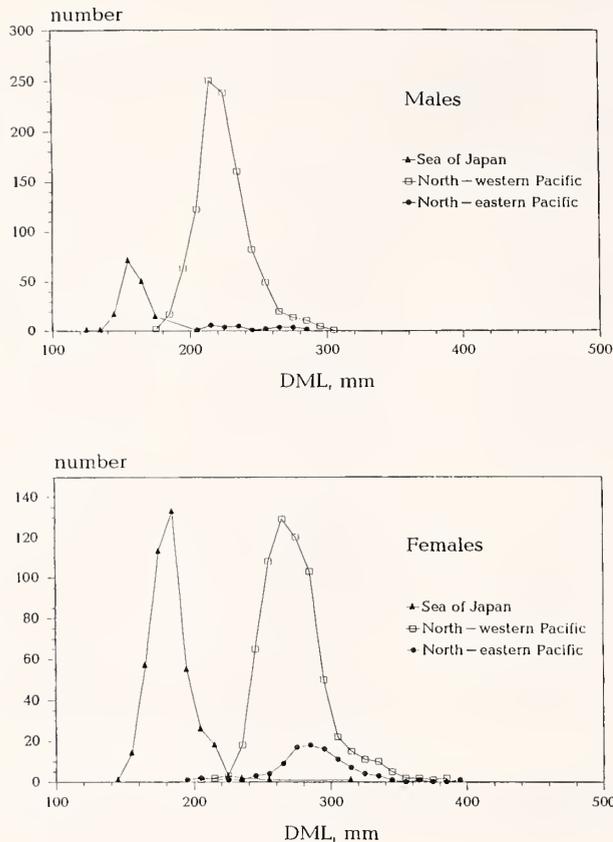
Figure 3

Berryteuthis magister. Size distributions for mature males and females from three regions in the North Pacific Ocean.

Figure 4

Berryteuthis magister. Relationship between dorsal mantle length (DML) and nidamental gland length (NGL) in mature females from three regions in the North Pacific Ocean. A. Distribution of individual values. B. Means and ranges by regions.

Second coefficient, which shows the angle of the regression line, is almost 1.5 times higher in Japanese samples than in the others, meaning that NGL is increasing more rapidly with DML in mature squid from the Japan Sea. This could be explained by the fact that the size distribution curve in mature *B. magister* from the Japan Sea is narrow with only one predominant class, whereas in the other regions, size distribution curves are wide, and composed of several size classes.

Fin Measurements and Indices

Measurements of fin length (FL) and fin width (FW), and indices of FL/DML and FW/DML varied considerably among samples of squid in different onthogenetic stages, and from different geographic regions.

For the samples from the northwestern Pacific the value of FL/DML rapidly increases in juveniles from 0.401 ± 0.006 (sample JB, DML = 54.9 ± 1.3) to 0.471 ± 0.007 (sample JO, DML = 100.1 ± 4.0), reaches a maximum of 0.495 ± 0.003 in immature adults (sample KU, DML = 197.0 ± 3.1), and slowly decreases to 0.489 ± 0.004 in prespawning squid (samples BS1 and BS2, DML = 250.7 ± 3.3) (Figure 5). Aleutian adults (sample AL,
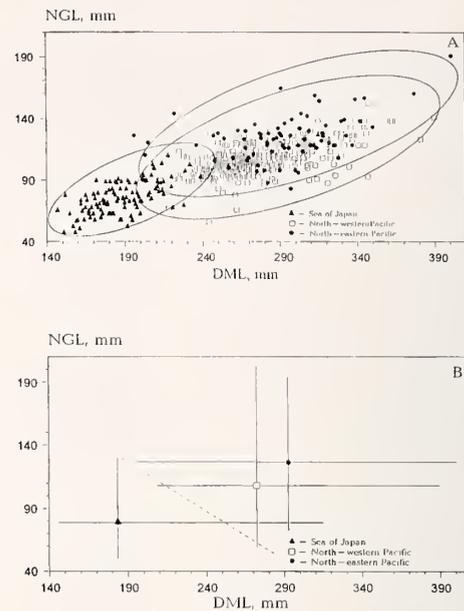
DML = 218.2 ± 12.4) have the shortest fins with a mean FL/DML index of 0.478 ± 0.004, while adults from the Japan Sea (sample JS, DML = 155.7 ± 6.7) are characterized by the highest average value of this index, 0.501 ± 0.006. Adult specimens from the Japan Sea lie between juveniles and immature adults on the graph of the FL index plotted against DML (Figure 5B).

For the samples from the northwestern Pacific the value of FW/DML slightly increases in juveniles from 0.759 ± 0.005 (sample JB) to a maximum of 0.805 ± 0.008 (sample JO), with a subsequent slow decrease through 0.718 ± 0.005 in immature adults (sample KU) to a minimum of 0.0.693 ± 0.004 in prespawning squid (samples BS1 and BS2) (Figure 6). Aleutian adults (sample AL) have a mean index value of 0.748 ± 0.008, which is intermediate between juveniles and immature adults from the northwestern Pacific. Adults from the Japan Sea (sample JS) are characterized by a mean FW/DML index of 0.771 ± 0.018, which falls between mean values for samples of juveniles and immature adults on the graph of this index plotted against DML (Figure 6B).

Radula

The radula of *B. magister* is of the heterodont type, and is characterized by seven teeth in a transverse row (versus five teeth in most other gonatids): rachidian tooth R, two lateral teeth L, two inner marginal teeth M1, and two outer marginal teeth M2. Based on nomenclature for
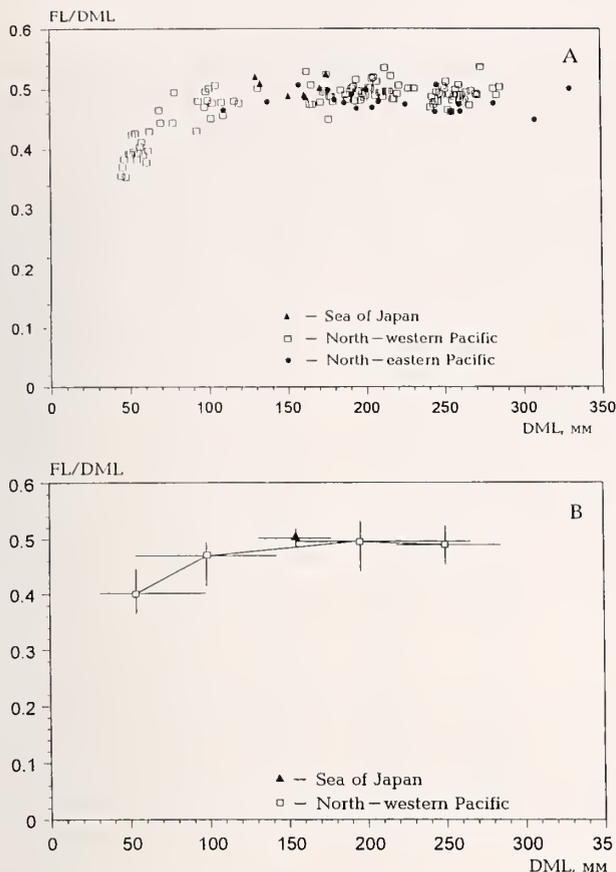
Figure 5

Berryteuthis magister. Relationship between fin length index (FL/DML) and dorsal mantle length (DML). A. Distribution of individual values. B. Means and ranges by regions.

cephalopod radulae, suggested by Nixon (1995), the radular formula for *B. magister* is represented as: R, -, L, M1, M2.

There are certain differences in radular morphology between *B. magister* from the Japan Sea, and from the northwestern Bering Sea (Figure 7). The rachidian tooth is essentially invariant, and consists of a mesocone with one lateral cusp on either side in all 50 adult animals studied. The lateral tooth on each side of the rachidian has one central cusp and one outer cusp in 22 of 25 specimens studied from the Japan Sea. In 18 of 25 studied specimens from the northwestern Bering Sea, there were three cusps on each lateral tooth: one large central cusp, one outer cusp, and a very small inner cusp. Three specimens from the Japan Sea had a tricuspid lateral, while seven specimens from the northwestern Pacific had a dicuspid lateral. None of the Japan Sea squid had a well-developed inner cusp on L. There was no visual correlation between a development of this cusp and a maturity stage in squid from any of two regions. All marginal teeth
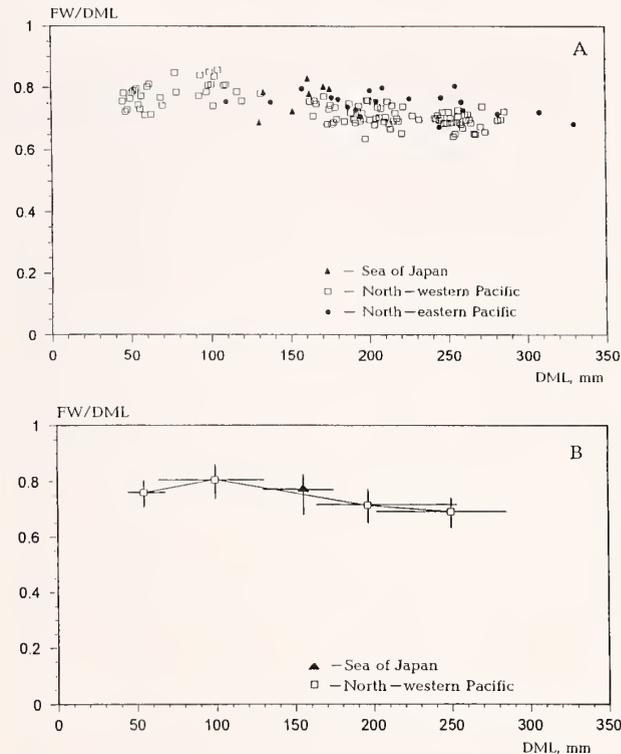

Figure 6

Berryteuthis magister. Relationship between fin width index (FW/DML) and dorsal mantle length (DML). A. Distribution of individual values. B. Means and ranges by regions.

in all specimens studied were unicuspid, as they are in most other Recent, and even fossil cephalopods (Nixon, 1995). Typical radular formulas for *B. magister* from the two different geographic regions would be: $_2R_2$, -, L_2, $M1_1$, $M2_1$ (for most of the specimens from the Japan Sea), $_2R_2$, -, L_3, $M1_1$, $M2_1$ (for most of the specimens from the northwestern Bering Sea).

Genetic Evidence

Genetic variation and differentiation between *B. magister* from the Japan Sea, and from the northwestern Pacific Ocean were assessed from the analysis of 26 putative genetic loci, coding for the enzymes and a polymorphic general protein zone. The following 12 loci had more than one allele present in at least one of the two samples: *Aat-2* (four alleles), *Est-2* (four alleles), *Fh-1* (five alleles), *Idh-1* (four alleles), *Ldh-2* (four alleles), *Mdh-2* (four alleles), *Mpi-1* (three alleles), *Pep-2* (four alleles), *Pgd* (five alleles), *Pgm-1* (four alleles), *Pnp* (three alleles), *Ugp* (two alleles) (Table 2). Fourteen loci were monomorphic in the Japan Sea sample, and 15 in the central Kurile sample. Genetic variability measures did not vary significantly between sampled populations from the Japan Sea and the Kurile region (Table 3). On aver-

Table 2

Berryteuthis magister: Genetic loci, alleles and allele frequencies for squid from the Japan Sea (sample JS) and north-western Pacific Ocean (sample CK). Number of specimens screened for each locus are given in brackets.

Locus Allele	Sample JS	CK	Locus Allele	Sample JS	CK	Locus Allele	Sample JS	CK	Locus Allele	Sample JS	CK
Aat-2	(51)	(130)	*Idh-1*	(102)	(130)	*Me*	(104)	(20)	*Pgm-1*	(63)	(133)
125	0.020	0.008	160	0.064	0.038	100	1.000	1.000	108	0.056	0.008
112	0.098	0.112	120	0.505	0.262	*Mpi-1*	(104)	(130)	105	0.175	0.120
100	0.873	0.881	100	0.387	0.654	120	0.034	0.000	100	0.746	0.805
88	0.010	0.000	85	0.044	0.046	100	0.962	1.000	97	0.024	0.068
Agp	(104)	(130)	*Idh-2*	(104)	(130)	75	0.005	0.000	*Pk-1*	(104)	(20)
100	1.000	1.000	100	1.000	1.000	*Mpi-2*	(104)	(130)	100	1.000	1.000
Ck	(104)	(20)	*Lap-1*	(104)	(20)	100	1.000	1.000	*Pk-2*	(104)	(20)
100	1.000	1.000	100	1.000	1.000	*Pep-1*	(104)	(130)	100	1.000	1.000
Est-1	(104)	(130)	*Lap-2*	(104)	(20)	100	1.000	1.000	*Pnp*	(103)	(130)
100	1.000	1.000	100	1.000	1.000	*Pep-2*	(101)	(125)	120	0.141	0.300
Est-2	(104)	(127)	*Ldh-2*	(103)	(130)	160	0.054	0.000	100	0.845	0.688
120	0.000	0.024	130	0.024	0.008	120	0.010	0.028	51	0.015	0.012
100	0.063	0.972	100	0.398	0.550	100	0.901	0.904	*Sod*	(104)	(130)
92	0.933	0.004	70	0.034	0.000	20	0.035	0.068	100	1.000	1.000
80	0.005	0.000	40	0.544	0.442	*Pgd*	(103)	(133)	*Ugp*	(111)	(130)
Fh-1	(99)	(130)	*Mdh-1*	(104)	(130)	103	0.019	0.026	100	0.847	0.781
155	0.061	0.046	100	1.000	1.000	100	0.961	0.932	85	0.153	0.219
125	0.086	0.046	*Mdh-2*	(103)	(107)	98	0.010	0.030			
100	0.798	0.873	115	0.073	0.121	95	0.010	0.004			
90	0.056	0.031	100	0.587	0.528	92	0.000	0.008			
40	0.000	0.004	75	0.340	0.341						
Gap	(104)	(20)	58	0.000	0.009						
100	1.000	1.000									

age, almost 40% of loci were polymorphic, and the observed heterozygosity values ranged from 0.128 in the Japan Sea to 0.137 in the Kuriles, which corresponded to the estimates, revealed earlier on a different sample of loci in *B. magister* from the northwestern Pacific (Katugin, 1993). Significant heterogeneity between the Japan Sea and Kurile samples of *B. magister* was revealed at seven of 12 loci: *Est-2, Idh-1, Ldh-2, Mpi-1, Pep-2, Pgm-1*, and

Table 3

Berryteuthis magister: Variability measures at 26 genetic loci in sampled populations of squid from the Japan Sea (sample JS) and north-western Pacific Ocean (sample Ck).

Variability measure	Population samples JS	CK
Mean sample size per locus	100.1 ± 2.5	99.4 ± 9.7
Mean number of alleles per locus	2.2 ± 0.3	2.1 ± 0.3
Percentage of polymorphic loci		
(0.95 criterion)	38.5	38.5
(0.99 criterion)	46.2	42.3
Mean heterozygosity per locus		
(biased estimate)	0.140 ± 0.038	0.135 ± 0.038
(unbiased estimate)	0.141 ± 0.039	0.135 ± 0.038
(direct-count estimate)	0.128 ± 0.035	0.137 ± 0.039

Table 4

Berryteuthis magister: Contingency comparison and fixation index F(ST) of squid from the Japan Sea and northwestern Pacific Ocean. Abbreviations: df—degrees of freedom; *Nal*—number of alleles; *P*—probability for the chi-square test; *—significant F(ST) value.

Locus	Nal	Chi-square	df	P	F(ST)
Aat-2	4	3.620	3	0.30554	0.001
Est-2	4	408.086	3	0.00000	0.825*
Fh-1	5	6.427	4	0.16947	0.007*
Idh-1	4	34.992	3	0.00000	0.057*
Ldh-2	4	18.859	3	0.00029	0.016*
Mdh-2	4	5.137	3	0.16203	0.003
Mpi-1	3	10.174	2	0.00618	0.017*
Pep-2	4	17.793	3	0.00049	0.006
Pgd	5	4.807	4	0.30763	0.003
Pgm-1	4	13.866	3	0.00309	0.007*
Pnp	3	16.474	2	0.00026	0.034*
Ugp	2	3.414	1	0.06465	0.007
Totals		543.648	34	0.00000	0.120*

Pnp (Table 4). Significant F(ST) values were observed at the following seven loci: *Est-2*, *Fh-1*, *Idh-1*, *Ldh-2*, *Mpi-1*, *Pgm-1*, and *Pnp*—and mean total value for 12 polymorphic loci was 0.12 (Table 4). Genetic divergence D_N between the two sampled populations of *B. magister* amounted to 0.044.

DISCUSSION

Comparative data from morphology (size distribution, fin measurements, radula), and genetics (electrophoretically detectable protein-coding loci) in *B. magister* revealed a pattern of intraspecific variation, which could be explained in terms of taxonomic and evolutionary relationships. Two independent sources of information showed that the population(s) from the Japan Sea differs significantly from conspecific populations in other regions of the North Pacific Ocean. Among morphologic indicators of the Japan Sea populations are: small body dimensions as revealed by distribution of DML, unimodality of size distribution for either sex, a comparatively large fin, and a radula with bicuspid lateral teeth.

The small size of *B. magister* from the Japan Sea is in good agreement with growth data as revealed by statolith microstructure analysis of specimens from the Rebun Bank (Japan Sea), and from the Kitamyamato Bank (Okhotsk Sea). Squid from the Japan Sea are characterized by a slow growth rate (based on growth curves), and by comparatively large hatchlings (based on two main radii of the natal ring) (Natsukari et al., 1993). Ripe oocytes from oviducts of mature females from the Japan Sea had a maximum diameter of 5.94 mm (Nazumi et al., 1979), which is almost 1.5 times larger than the size of oocytes (4.2 mm) from the western Bering Sea specimens

(Fedorets & Kozlova, 1986). Small body size and large oocytes result in low individual fecundity of *B. magister* from the Japan Sea, with a maximum number of eggs of nearly 4000 per female (Nazumi et al., 1979), while the maximum number of eggs per ripe female in the western Bering Sea amounted to 29,000 (Fedorets & Kozlova, 1986), which is almost seven times higher. Comparatively low individual fecundity of the species in the Japan Sea could be due to onthogenetically involved reproductive features, such as dynamics of oocyte formation and development. It was shown that the germinative epithelium with gonial cells continues to produce future oocytes in fully mature females of *B. magister* from the northwestern Pacific (Reznik, 1982). Small size of females from the Japan Sea could be due to a slow growth rate and/or early maturation. If the latter is the case, then egg production and consequently, individual fecundity will be lower in smaller females from the Japan Sea, and higher in larger females from the northwestern Pacific. Low fecundity, combined with the production of eggs with a higher yolk content, (the increase of egg diameter from 4.2 to 5.94 mm theoretically results in a nearly three-fold increase of yolk content) should lead to an increased survival rate for paralarvae in the rather specific oceanologic conditions of the Japan Sea. Higher survival rates for animals with a higher content of egg yolk is due to the so-called effect of embryonization (Zakhvatkin, 1975). In such cases, a hatchling is born with more developed features, and hence more prepared for life, than a hatchling with lower yolk content. Reproductive strategies of *B. magister* from the Japan Sea encompass, particularly, time and longevity of spawning season. In this region, the spawning season of squid is more restricted in time, judging by the period of hatch, assessed from statoliths analysis (Natsukari et al., 1993), and is confined to spring with a single peak (Yuuki & Kitazawa, 1986). In the northwestern Pacific, spawning of *B. magister* is much more extended, and covers a long period from summer through autumn, terminating in winter, with at least two peaks (Fedorets, 1983; Kubodera, 1982, 1992; Nesis, 1995).

Squid from the northwestern and northeastern Pacific are hardly distinguishable based on external morphology (radulae have not been studied in specimens from the northeastern Pacific). Distributions of DML and NGL could be measured by a Coefficient of Difference, CD,— a formal descriptor of a subspecific differentiation between conspecific populations (Mayr, 1969). The critical value of subspecific differentiation is at CD of approximately 1.28, when 90% of specimens from one population differ from 90% of specimens from the other population. CD values between specimens from the northwestern and northeastern Pacific were 0.37 for DML, and 0.66 for NGL, which is considerably lower than the critical value of 1.28, and corresponds to the maximum nonoverlap of 74% between character distribution curves. At

Table 5

Intraspecific normalized genetic identity, I, and standard genetic distance, D_N (Nei, 1972), for different species of squid (L—number of genetic loci).

Taxon	Evolutionary divergence	L	I	D_N	Reference
Illex argentinus	populations	25	0.979–1.000	0.021–0.000	Carvalho et al. (1992)
	sibling species	25	0.878–0.904	0.130–0.101	Carvalho et al. (1992)
Martialia hyadesi	populations	39	0.998–0.999	0.002–0.001	Brierley et al. (1993)
	sibling species	39	0.508–0.509	1.790–1.775	Brierley et al. (1993)
Todarodes pacificus	populations	11	0.997–1.000	0.003–0.000	Kim (1993)
Loligo vulgaris	subspecies	18	0.970	0.030	Augustyn & Grant (1988)
Loligo forbesi	populations	33	0.998	0.002	Brierly et al. (1993)
	geographical populations	33	0.898–0.902	0.108–0.103	Brierly et al. (1993)
Loligo gahi	populations	21	0.997–1.000	0.003–0.000	Carvalho & Pitcher (1989)
Berryteuthis magister	populations	4	0.989–1.000	0.011–0.000	Katugin (1995)
	populations	19	0.999	0.001	Katugin (1993)
	geographical populations	4	0.980–0.998	0.020–0.002	Katugin (1995)
	(subspecies)	26	0.957	0.044	(this paper)

the same time, specimens from the Japan Sea differ from the others with CD values of 2.28 for DML, and 1.47 for NGL, which corresponds to more than 93% of nonoverlap between character distribution curves. Gaps in distributions of each of the two morphometric characters suggest that *B. magister* populations from the Japan Sea differ from conspecific populations from other parts of the species range on a subspecific level.

It was shown earlier that genetic differences between spatially isolated populations of *B. magister* from the northwestern Pacific, as revealed by Nei's (1972) genetic distance (D_N), were very small, of 0.001 (Katugin, 1993). Genetic divergence between conspecific populations of *B. magister* from the Japan Sea and from Pacific waters off the Kuriles appeared to be 44 times higher: $D_N = 0.044$. This estimate is slightly higher than the genetic distance between two African subspecies of *Loligo*: *L.* (*vulgaris*) *vulgaris,* and *L.* (*v.*) *reynaudii* (Augustyn & Grant, 1988) (Table 5). When approximated on a time scale, the estimate of $D_N = 0.044$ corresponds to the time of evolutionary divergence between populations of 220,000 years (Nei, 1987). It means that *B. magister* populations in the Japan Sea were isolated from the ancestral northwestern Pacific conspecific populations during the Riss glaciation period (Meso-Pleistocene, 250,000–125,000 years ago). Presumably, during the Riss and Vurm Periods, the Japan Sea Basin was disconnected from adjacent northwestern Pacific waters. During one of the latest interglacial transgressions of the sea level, the Japan Sea territory was colonized by various species of the boreal Pacific fauna through a channel through the middle of modern Sakhalin Island (Nishimura, 1964). Colonization events probably included ancestors of *B. magister*. Chains of islands, which were formed during sea level regressions, likely served as barriers to gene flow between founder and parental populations. Apparently, these barriers were effec-

tive for a nectobenthic bathypelagic species such as *B. magister*. Hydrological conditions in the recently formed sea basin, which were different from those of the northwestern Pacific, served as strong selective forces. As a result, a specific ecomorphotype of *B. magister* evolved with an effective reproductive strategy. Low temperature and geographic isolation of squid in the Japan Sea were presumably among possible triggers for maturation at smaller size, and consequently for evolving of a pedomorphic line of *B. magister*. Pedomorphic subspecies are known among living and fossil animals, and are most likely to be formed on a periphery of a species range as a response to regular changes in environment (Eldredge & Gould, 1972; Raff & Kaufman, 1983). Interpopulation (intersubspecific) genetic differences were acquired during a long and effective geographic isolation of *B. magister* in the Japan Sea. The absence of gene flow between the Japan Sea and adjacent *B. magister* populations is confirmed by the high F(ST) value of 0.12, and corresponding estimate of theoretical number of only two migrants per generation. It means that two specimens per generation are required to maintain the observed value of genetic differentiation. For very large effective population sizes of millions of animals, the estimate of two migrants in each generation means that there is almost no contact (gene exchange) between populations. At the same time, a D_N value of 0.044 is comparatively small and does not indicate that these populations represent two different species. Typically, for sexually reproducing organisms with an allopatric model of speciation, which is most likely to be the case in *B. magister,* Nei's (1972) genetic distance values between closely related species fall around 0.7–0.8 (Ayala, 1983).

All facts suggest that populations of *B. magister* from the Japan Sea have acquired a subspecific level of evolutionary and taxonomic divergence. Subspecific status of
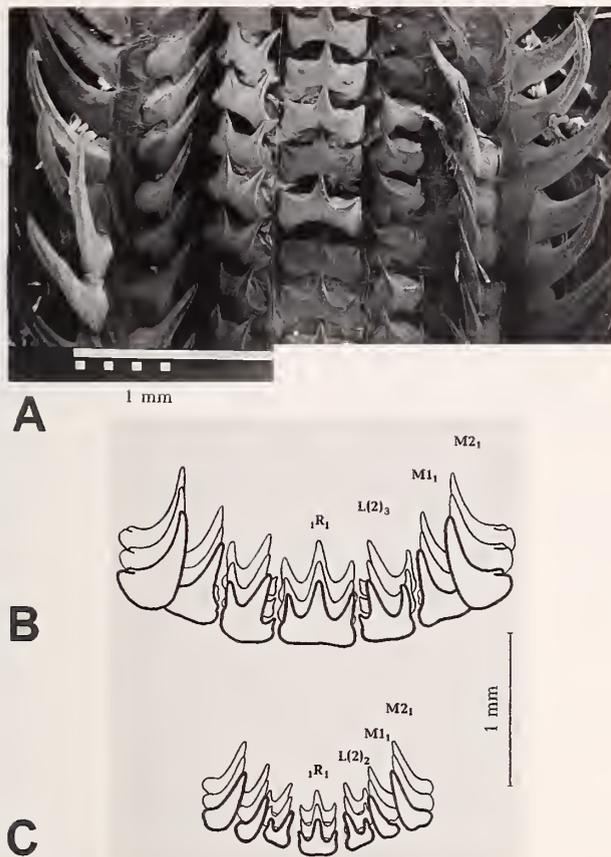
A

1 mm

B

M2₁ → $M2_1$

C

Figure 7

Radula of *Berryteuthis magister*. A. Maturating male (stage III; 214 mm DML) from the western Bering Sea, SEM photo, magnification 70X. B. Diagram for the same specimen. C. Mature male (stage V, 134 mm DML) from the Japan Sea, diagram.

B. magister from the Japan Sea satisfies the following criteria: (1) geographical isolation; (2) specific habitat (hydrological conditions); (3) characteristic traits in general morphology (body size, fin proportions, club armature, radula); (4) certain peculiarities in reproductive traits (egg size and fecundity) and behavior (spawning time and dynamics); and (5) significant differentiation at structural genetic loci.

DESCRIPTION OF A NEW SUBSPECIES OF *B. MAGISTER*

Based on morphological, genetic, reproductive, and ecological data, I propose a new taxon of a subspecific rank. The formal description for a new subspecies of the gonatid squid *B. magister* from the Japan Sea is presented below.

Table 6

Berryteuthis magister shevtsovi Katugin, subsp. nov: Principal measurements (mm) and indices for holotype and paratype. Diagrammatic illustrations of measurements are given in Figures 8, 10, and 11.

Character	Holotype	Paratype
Catalog No	BMJS001	BMJS002
sex	male	female
maturity stage	V	III
DML	162	172
MW (MWI)	59 (36.4)	57 (33.1)
FL (FLI)	79 (48.8)	86 (50.0)
FW (FWI)	134 (82.7)	138 (80.2)
HW (HWI)	41 (25.3)	33 (19.2)
ED (EDI)	22 (13.6)	20 (11.6)
TTL (TTLI)	255 (157.4)	231 (134.3)
SZL	117	—
CLDL	71	—
CLVL	51	—
CLWL	21	19
CLMW	11	9
AI AL (AILI)	99 (61.1)	94 (54.7)
A	8	8
B	14	16
C	49	48
D	28	22
AII AL (AIILI)	107 (66.0)	110 (64.0)
A	15	14
B	16	16
C	53	50
D	23	30
AIII AL (AIIILI)	114 (70.4)	108 (62.8)
A	17	16
B	12	13
C	59	54
D	26	25
AIV AL (AIVLI)	105 (64.8)	99 (57.6)
A	15	14
B	16	—
HCL	31	—
D	28	—
AIV FA	105	—

Berryteuthis magister **shevtsovi** Katugin, subsp. nov.

(Figures 7–11, Tables 6, 7)

Material examined: Seven adult specimens were screened for variation in morphologic traits; two of them were in fairly good condition, and hence selected as type specimens. *Holotype:* male (mature, stage V), 162 mm DML; *paratype:* female (maturating, stage III), 172 mm DML (from the same haul as holotype). Deposition of the type specimens: collection of cephalopods, laboratory for squid research, Pacific Research Fisheries Centre (TIN-

Table 7

Comparison of character states for different subspecies of *Berryteuthis magister*. Abbreviations: DML—dorsal mantle length; NGL—nidamental gland length; FLI—fin length index; FWI—fin width index; radula teeth: R—rachidian, L—lateral, M1—first marginal, M2—second marginal; d(centr)—diameter of largest sucker ring (central region of the manus); d(marg)—diameter of smallest sucker ring (marginal region of the manus).

| | Subspecies | | |
| | *shevtsovi* (new) | *magister* (nominotypical) | *nipponensis* (Japanese) |
Character			
Maturity (stage)	mature (IV–V)	mature (IV–V)	immature (II)
DML—males (mm)	129–202	177–302	182*
mean	150.26 ± 0.73	224.85 ± 4.49	
DML—females (mm)	147–315	209–390	
mean	184.23 ± 0.78	273.48 ± 0.91	
NGL (mm)	50–129	58–202	no data
mean	78.22 ± 0.55	107.13 ± 0.45	
FLI	0.485–0.523	0.445–0.512	
mean	0.501 ± 0.006	0.486 ± 0.004	(0.500)*
FWI	0.687–0.827	0.643–0.739	
mean	0.771 ± 0.018	0.695 ± 0.005	0.643*
Differences between central and marginal club suckers	weak	pronounced	weak*
d(centr)/d(marg)	1.6–2.0	2.0–2.8	
Typical radula	$_1R_1$-L_2 $M1_1$ $M2_1$	$_1R_1$-L_3 $M1_1$ $M2_1$	no data
lateral tooth	dicuspid	tricuspid	
Maximum individual fecundity (number of eggs)	3755	25,000	no data
Largest egg diameter (mm)	5.94	4.20	no data
Sea temperature (°C)	0.3–0.5	3.0–4.0	no data
Ecotype	quasibenthic stenobathic	quasibenthic stenobenthic	eurybathic(?)
Breeding season	spring	summer, autumn	no data

* Holotype (Okutani et al., 1987).

RO-Centre), Vladivostok, Russia. *Holotype:* BMJS001. *Paratype:* BMJS002.

Type locality: Type specimens were collected by Pavel V. Kaltchugin on the Russian research vessel *Professor Kaganovskyi* from the continental slope of the Japan Sea (Russian Primorie region, 42°30'N, 133°42'E); bottom trawling station; 600 m deep; 23 May 1996.

Diagnosis: Subspecies small (fully mature females usually to 200 mm DML, mature males usually to 170 mm DML); fin long (to 50% of DML) and wide (to 77% of DML); poorly shaped, and weakly differentiated hookless tentacular club; small differences between central and marginal suckers on the manus of the club; fixing apparatus undifferentiated, consists of almost 40 elements (42 pads alternating with minute hookless suckers in holotype), starts from approximately central dorsal part of the stalk, and terminates on distal part of the manus; bicuspid lateral teeth of the radula.

Description: *Body* (Figure 8). Small to medium size.

Dorsal mantle length (DML) of mature prespawning females usually does not exceed 180–200 mm, Mature males usually do not exceed 140–170 mm.

Mantle. Cylindrical; width (MW) approximately 1/3 of DML: MW 36% of DML for holotype. Anterodorsal margin of mantle with triangular projection; small in immature adults, well-defined in prespawning and spawning animals. Anteroventral mantle edge slightly emerginate with two small lateral angles which border funnel.

Fin. Rhomboid, large; length (FL) about 50% of DML, width (FW) almost 80% of DML. Anterior and posterior fin margins straight; anterior lobes of fin distinct; lateral margins slightly rounded.

Head. Cubic and large; slightly smaller than mantle opening. Head width index (HWI) 25% in holotype. Eyes large, with long, deep sinus; eye diameter index (EDI) about 14% in holotype.

Funnel organ (Figure 9). Composed of dorsal element (DFO) and two smaller ventral elements (VFO). Dorsal pad large, A-shaped. Both limbs of DFO joined anteri-
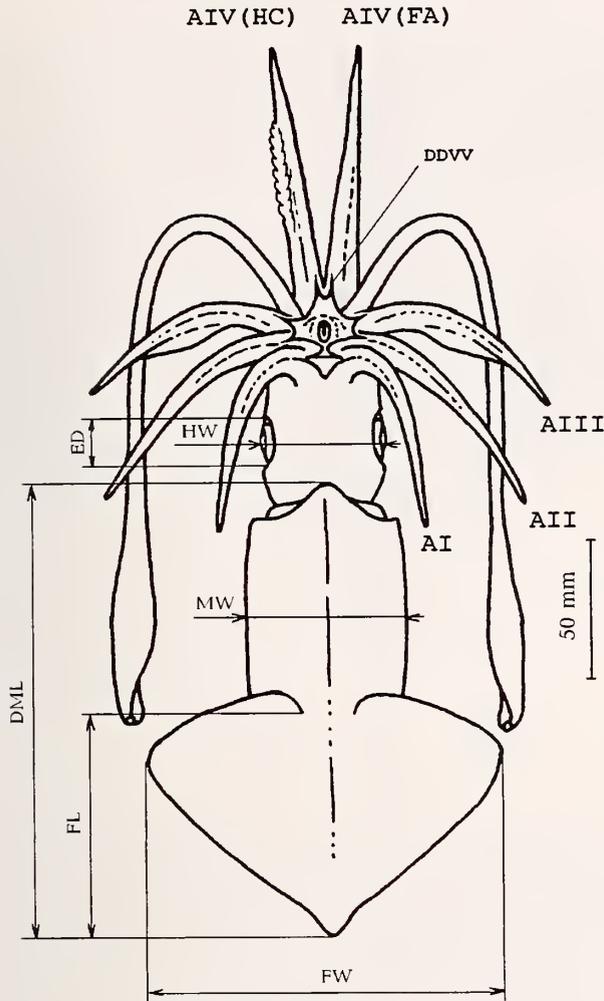
Figure 8

Berryteuthis magister shevtsovi Katugin, subsp. nov. Dorsal view of the holotype. DDVV, type of buccal lappets attachment (Dorsal, Dorsal, Ventral, Ventral); AI–AIV, arms one to four; HC, hectocotylized arm; FA, fellow arm; DML, dorsal mantle length; MW, mantle width; HW, head width; ED, eye diameter; FL, fin length; FW, fin width.

orly; apex bifurcal. Total length of DFO almost 15% of DML in holotype. Ventral pads oval, 2/3 length of DFO.

Mantle locking apparatus (Figure 9). Consists of nuchal cartilage (NC), and funnel cartilages (FC). Nuchal cartilage elongated, slightly broader proximally, with median and two lateral grooves; length nearly 12% of DML. Funnel locking-cartilage lanceolate with median sulcus anteriorly; flat and expanded posteriorly; length almost 14% of DML in holotype. Mantle cartilages (MC) which correspond to funnel cartilages consist of low ridges which expand posteriorly.

Arms (Figure 10A, B). Muscular and long; longest arm 70%, and shortest 61% of DML in holotype. Arm for-
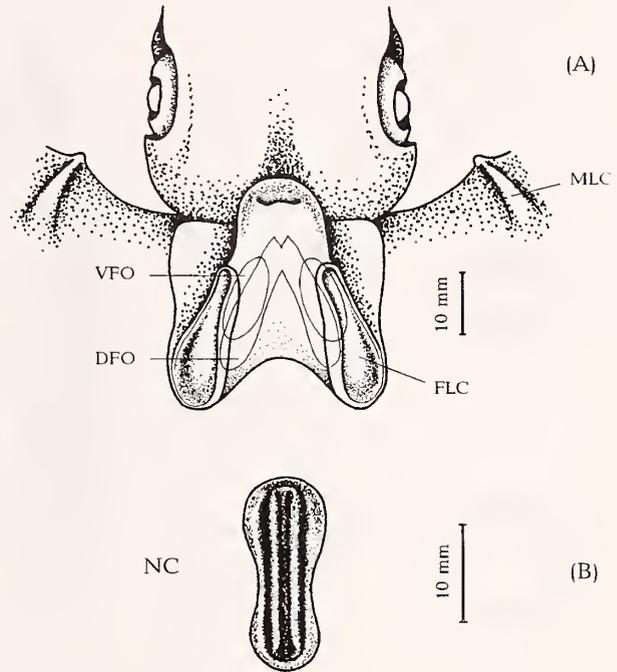

Figure 9

Berryteuthis magister shevtsovi Katugin, subsp. nov. Head, locking cartilages, and funnel organ. A. Ventral view (mantle is opened). MLC, mantle locking cartilage; FLC, funnel locking cartilage; DFO, dorsal funnel organ (inside the funnel); VFO, ventral funnel organ (inside the funnel). B. Nuchal cartilage (NC).

mula typical for species: III>II>I>IV. Aboral swimming keel well developed on third arm, less evident on other arms. Arms equipped with tetraserial armature. Armature in four longitudinal rows (ventral, medioventral, mediodorsal, and dorsal). Basal or proximal regions of all arms lack armature; first suckers appear on ventral and dorsal rows; distal parts of all arms with minute suckers alone. Ventral arms (AIV) with suckers only. In adult males central or medial region of one of arm IV pair modified as hectocotylus (HC); opposite ventral or fellow arm (FA) not modified. Females lack modifications on arms IV. Arms I, II, and III bear suckers in ventral and dorsal rows and hooks in central regions of medioventral and mediodorsal rows. In each central row five to six suckers present, followed by 11 to 13 hooks. Number of hooks on arms I, II, and III in holotype 22, 24, and 26, respectively. Overall numbers of transverse rows of armature on arms I–IV in holotype 31, 32, 37, and about 40, respectively.

Hectocotylus. Modifications confined to medial region of one ventral arm only; proximal third and distal third of arm appeared unmodified (Figure 10A, B). Suckers in dorsal and mediodorsal rows differ in size and form, while suckers in medioventral and ventral rows remain unchanged. Modified sucker stalks of both rows suffi-
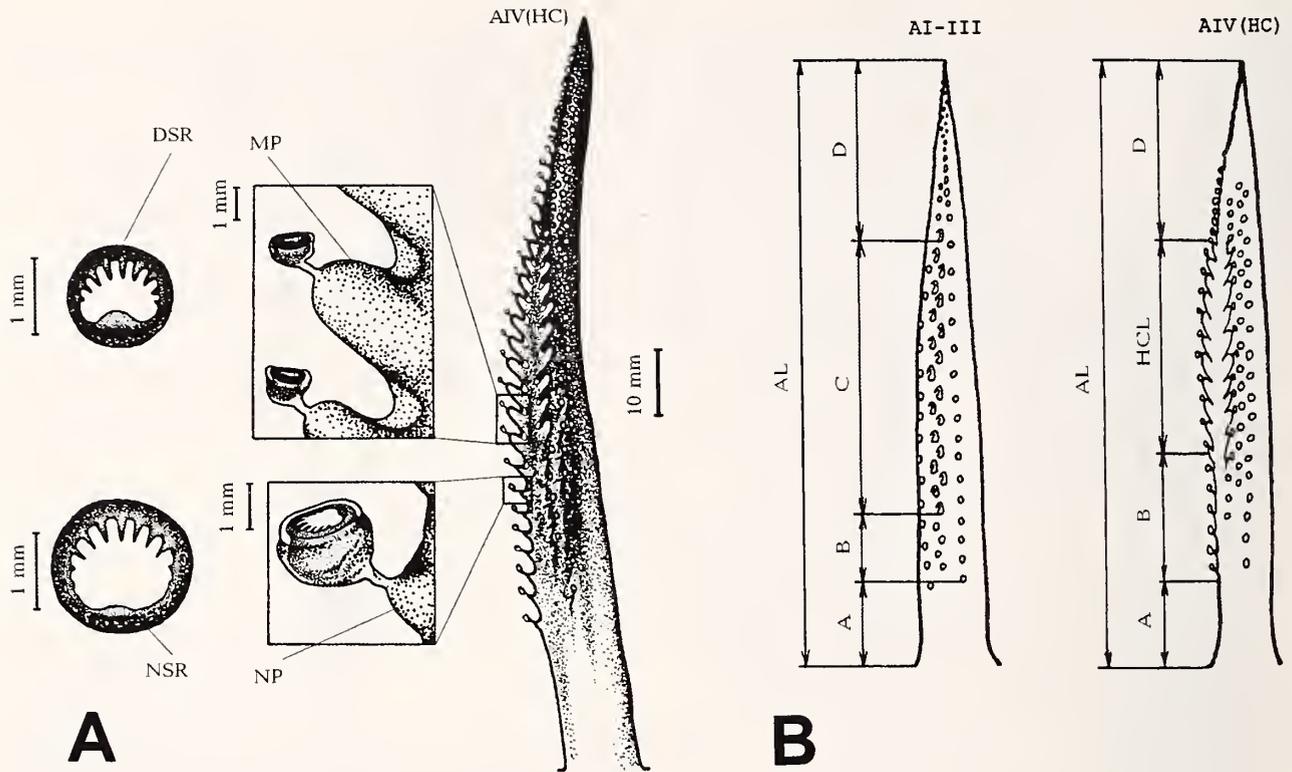
Figure 10

Berryteuthis magister shevtsovi Katugin, subsp. nov. A. Hectocotylized ventral arm of the holotype specimen. AIV(HC), ventral view of the arm; NP, unmodified sucker (enlarged); NSR, unmodified sucker ring (enlarged); MP, modified sucker (enlarged); DSR, modified sucker ring (enlarged). B. Diagram of arm measurements: AI–III, arms one to three; AIV(HC), arm four (hectocotylized arm); AL, arm length; A, basal region without suckers; B, proximal suckers zone; C, hooks zone; D, distal suckers zone; HCL, zone with modified suckers.

ciently enlarged to form narrow groove. Sucker modifications in fully mature and prespawning males much more conspicuous than in immature and maturating specimens. Left ventral arm modified in holotype and two specimens; in all others right ventral arm modified. Hectocotylus of holotype described below. First eight suckers in dorsal row, and first six suckers in mediodorsal row appear almost unmodified, except some thickening at base of sixth and eighth sucker stalks. Noticeable changes evident in 11 succeeding suckers (rows 9–19) in dorsal row, and in ten succeeding suckers (rows 7–16) in mediodorsal row. Papilla formed by stalk base of each modified sucker, 5–6 mm high; sucker pedicel (stalk upper part) short, about 1 mm in length; sucker ring almost two times smaller than that of unmodified sucker. Number of unmodified proximal, and affected central suckers varies among specimens, six to nine and eight to twelve in dorsal row; six to eight and six to nine in mediodorsal row.

Ventral arm modifications in *B. magister* were first described as a true hectocotylus in several mature males from the northeastern Pacific, and Bering Sea by Voight (1995). Such arm modifications in males of *B. magister*

from the Japan Sea are herein reported for the first time. Holotype and ten males of squid in various maturity stages (II–V) were analyzed. All specimens, except one immature (stage II) male, had noticeable morphological changes on one of the ventral arms.

Tentacles (Figure 11A, B). Long, narrow, almost 1.5 times longer than mantle length. Tentacle total length (TTL) of holotype 157% of DML. Club elongated, lanceolate; maximum width (CLMW) 4% of TTL. All club regions (e.g., carpal zone, manus, and dactylus) weakly defined (Figure 11A). Principal measurements made based on attachment of club membranes (Figure 11B). Boundary between dactylus and manus roughly corresponds to beginning of apical aboral membrane on outer surface of club; relative length of dactylus (CLWL/TTL) 8.2% in holotype. Proximal boundary of manus corresponds to starting point of ventral membrane; length of this membrane (CLVL) 20% of TTL in holotype; ratio of manus length to TTL 11.8%. Proximal attachment of dorsal membrane corresponds to boundary between club and stalk; length of this membrane (CLDL), and thus club length, 28% of TTL, and 44% of DML in holotype. Car-
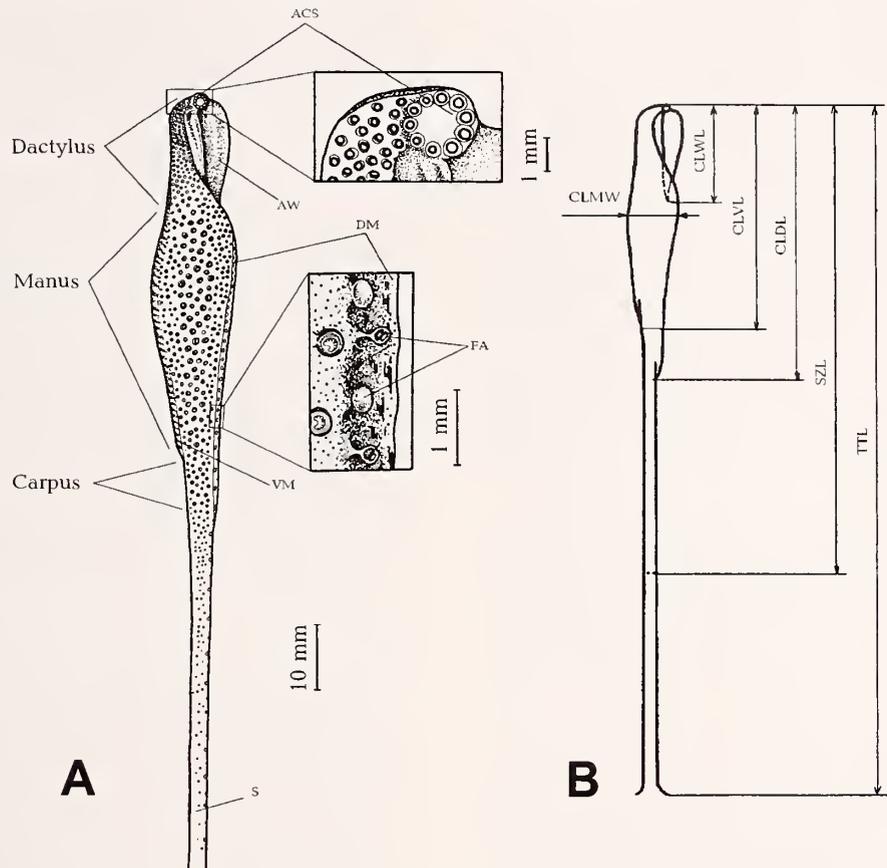
Figure 11

Berryteuthis magister shevtsovi Katugin, subsp. nov. A. Tentacle of the holotype specimen with details of the club (carpus, manus, and dactylus). S, distal part of the stalk; ACS, apical circlet of suckers; AW, aboral web; DM, dorsal membrane; FA, fixing apparatus (enlarged are two pads, and two alternating toothless suckers); VM, ventral membrane. B. Diagram of tentacle measurements: TTL, total tentacle length; SZL, suckers zone length; CLDL, club dorsal length (from the place of dorsal membrane attachment); CLVL, club ventral length (from the place of ventral membrane attachment); CLWL, club aboral web length; CLMW, club maximum width.

pal zone covers about 8% of holotype TTL, and somewhat less, than 30% of club length. Sucker zone length (SZL) occupies almost 46% of TTL in holotype.

Circlet of minute suckers at tip of tentacle (Figure 11A); ten suckers on right tentacle, and 11 suckers on the left; circlet diameter 2.4 mm in holotype. Sucker rim without teeth; diameter of sucker rim ranges from 0.3–0.6 mm. Proximal to apical circle transverse rows of suckers present on inner surface of dactylus. Two distalmost sucker rows tetraserial; number of suckers in each transverse row increases proximally. Suckers toothless to central part of dactylus where bluntly pointed teeth first appear. Largest suckers in central part of manus; maximum ring diameter 0.6–0.75 mm. Small suckers cover dactylus, borders of manus, carpal zone, and proximal stalk; minimum diameter of rim of sucker from ventral margin of manus 0.3–0.32 in holotype; ratio of largest to smallest rim diameter range from 1.6–2.0 in holotype.

Fixing apparatus (Figure 11A). Extends to dorsal edge of tentacle, starting from first suckers on stalk, and terminating on border between manus and dactylus. Locking zone consists of alternating series of pads (or knobs) and minute toothless suckers. Knob diameter 1.5–2 times larger than sucker ring diameter; number of knobs approximately 40 in holotype.

Distribution and habitat: The range of *B. (m.) shevtsovi* is presumably limited to the Japan Sea, and data on distribution and ecology of *B. magister* in this region could be applied to the new subspecies as well. This squid has been reported between the Oki and Tsushima groups of islands (35°25′N, 130°35′E, E. V. Slobodskoy, personal communication), hence the southernmost boundary of distribution presumably goes through the Korean Strait. It is widely distributed throughout the Japan Sea, with large stocks reported from the Jamato Bank, Kitayamato

Bank, Sinoki Bank, Rebun Bank, and from the Oki and Noto Seamounts (Ogata et al., 1973; Kasahara et al., 1978; Nazumi et al., 1979; Natsukari et al., 1993; Shevtsov, 1988). The northernmost boundary is in the Tatarsky Strait (Railko, 1979). Vertical distribution of the squid in the Japan Sea is uneven. Adults are confined to the slope depths. Specimens of various maturity stages ranged in depth from 50–1200 m with a maximum occurrence of adults in depths 300–500 m, which is characteristic of the species (Kubodera, 1982, 1992; Okiyama, 1993; Railko, 1979). Habitat is determined by rather specific hydrological conditions of the Japan Sea, when compared to the subarctic hydrology of the rest of the northern Pacific Ocean (Okiyama, 1993; Kitano, 1958). The most notable feature of the squid's habitat in the Japan Sea is low temperature, in the range of 0.2–1.5°C (Okiyama, 1993; Railko, 1979).

Etymology: In honor of Dr. Gennadyi A. Shevtsov, eminent Russian researcher for the North Pacific cephalopods, particularly for the cephalopods from the Japan Sea.

Comparative morphologic, reproductive, and ecologic features for the three subspecies of *B. magister*, namely *B. (m.) magister*; *B. (m.) nipponensis*; and *B. (m.) shevtsovi* are presented in the Table 7.

Taxonomic summary: *B. (m.) shevtsovi* is distinguishable both from *B. (m.) magister*, and from *B. (m.) nipponensis*, though as expected, morphological intersubspecific differences are rather quantitative. There are virtually no diagnostic morphologic characters, which could unambiguously (with a 100% probability of correct diagnosis) distinguish among all the three subspecies. Mature adults of *B. (m.) shevtsovi* are considerably smaller, have a comparatively larger fin, and less pronounced differences between central and marginal club suckers than mature specimens of *B. (m.) magister*. Most specimens of the new subspecies possess bicuspid lateral teeth of the radula, while there are three cusps on the same teeth in the majority of specimens of the nominotypical subspecies from the Bering Sea. It is rather hard to compare taxonomic characters of *B. (m.) shevtsovi* with those of *B. (m.) nipponensis*, because the latter was described from immature specimens with undeveloped traits of external morphology. We can guess though, that basic differences between these taxa are in body size (the new subspecies is considerably smaller), in fin size (the new subspecies has a larger fin), and in mantle width (the new subspecies has a wider mantle with pallial aperture larger than head width). All the three subspecies also differ in ecological characters, *B. (m.) magister* being stenobathic, *B. (m.) shevtsovi*—cold-water stenobathic, and *B. (m.) nipponensis*—presumably eurybathic.

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